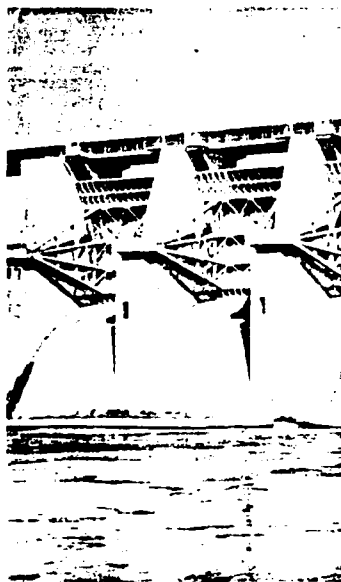




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TECHNICAL REPORT EL-89-10

SPECIES PROFILES: LIFE HISTORIES AND ENVIRONMENTAL REQUIREMENTS OF COASTAL VERTEBRATES AND INVERTEBRATES PACIFIC OCEAN REGION

Report 4

THE HAWAIIAN ANCHOVY OR NEHU
ENCRASICHOLINA PURPUREA (ENGRAULIDAE)

by

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November 1989

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<p>➤ The nehu is a small anchovy restricted to semienclosed areas in Hawaii for most of its life cycle; some evidence indicates that nonspawning adults may move into exposed coastal habitats. Spawning occurs throughout the year but is concentrated between late summer and early winter. Incubation and development to first-feeding status require only a few days. The larvae metamorphose at a standard length of about 30 mm and an age of about 90 days. Sexual maturity occurs at 35 to 40 mm, and maximum size and age are about 65 mm and 6 months, respectively.</p> <p>Late larval, juvenile, and adult nehu typically occur in shallow areas by day and migrate into deeper water to feed at night. The diet is dominated by large zooplankton with apparent preference for crustaceans. Nehu are eaten by a variety of predators, mostly fishes. They are the major source of bait for the Hawaiian skipjack tuna fishery. Available analyses of catch and effort data give no clear evidence that the fishery has seriously impacted the population.</p> <p style="text-align: right;">(Continued)</p>					
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Based on estimates of nehu consumption rates, standing crops, and fishery yields, it appears that nehu consume a large fraction of zooplankton production in semienclosed habitats in Hawaii. The physiological tolerance ranges of nehu indicate that they probably only rarely encounter deleterious conditions in nature and have, as yet, probably not been seriously impacted by human activity in coastal situations. (C)

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PREFACE

This report is designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the Hawaiian anchovy or Nehu, *Engrasicholina purpurea* and to describe how populations of the species in Hawaiian waters may be expected to react to environmental changes caused by coastal development. This report has sections on taxonomy, life history, ecological role, environmental requirements, growth, exploitation, and management.

This work was part of the Environmental Impact Research Program (EIRP), sponsored by Headquarters, US Army Corps of Engineers (HQUSACE), under EIRP Work Unit 31627. Technical Monitors were Dr. John Bushman, Mr. David P. Buelow and Mr. David Mathis of HQUSACE.

This report was prepared by Dr. Thomas A. Clarke of the Department of Oceanography and Hawaii Institute of Marine Biology, University of Hawaii.

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CONVERSION TABLE

Metric to U.S. Customary

<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m ²)	10.76	square feet
square kilometers (km ²)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m ³)	35.31	cubic feet
cubic meters (m ³)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft ²)	0.0929	square meters
square miles (mi ²)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft ³)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

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THE HAWAIIAN ANCHOVY OR NEHU, ENCRASICHOLINA PURPUREA (ENGRAULIDAE)

NOMENCLATURE/TAXONOMY/RANGE

Scientific name Encrasicholina purpurea (Fowler)
Preferred common name Nehu
Class Osteichthys
Order Clupeiformes
Family Engraulidae

Geographic range: Nehu are restricted to the Hawaiian Islands.

INTRODUCTION

The Hawaiian anchovy or nehu, Encrasicholina purpurea, is the dominant small pelagic fish in enclosed, semiestuarine areas of Hawaii and is also the major source of live bait for the Hawaiian skipjack tuna fishery. As such, it has been the object of a relatively large number of research studies. Much of the work on nehu was done in the 1950's and was reviewed by Nakamura (1970). More intensive studies using modern techniques were begun in the early 1980's in Kaneohe Bay by the University of Hawaii, Hawaii Institute of Marine Biology, and more recently in Pearl Harbor by the National Marine Fisheries Service Honolulu Laboratory. These recent programs have greatly increased knowledge of nehu biology and ecology and also have superseded or made equivocal some conclusions

reached by earlier studies. Consequently, this report will make frequent use of unpublished and, in some cases, preliminary conclusions of ongoing research.

SYSTEMATICS

Nehu are anchovies (Family Engraulidae) that were formerly included in the Indo-Pacific genus Stolephorus (Gosline 1951). Based on osteological characters, Nelson (1983) placed nehu and four other species of Stolephorus in the genus Encrasicholina.

The only other anchovy that occurs in Hawaii is the congener Encrasicholina punctifer, which was first recorded from Hawaii and described as a new species, Stolephorus buccaneeri, by Strasburg (1960). Wongratana (1983) showed that S. buccaneeri was identical with E. punctifer, one of the five species included in Encrasicholina by Nelson (1983). Strasburg's (1960) description purported to show that nehu could be differentiated from E. punctifer by several morphometric characters, but both Matsui (1963) and current unpublished data indicate that features such as relative head length, etc., of nehu are extremely variable and can overlap with those of E.

punctifer. The most reliable character for separating the two species appears to be the relative lengths of pectoral fins; these reach over half the distance between the pectoral and pelvic bases in nehu, but are much shorter in E. punctifer. Characters useful in separating larvae of the two species are given in Miller, Watson, and Leis (1979).

DISTRIBUTION AND HABITAT

Nehu are endemic to the Hawaiian Islands. They appear to be restricted to enclosed, semiestuarine areas for all but the adult stages. The two largest such areas in Hawaii are Kaneohe Bay and Pearl Harbor, both on the island of Oahu.

Spawning and the egg and larval stages apparently occur only in enclosed areas. Besides the two major habitats given above, eggs have been reported only from the Ala Wai canal (Tester and Yamashita 1950), but it is likely that some spawning also occurs in other smaller, partially enclosed areas such as Honolulu Harbor and Hilo Harbor. Recently a few anchovy eggs were taken in plankton tows off exposed coasts. These may have resulted from either occasional spawning of nehu offshore or dispersal of nehu eggs from enclosed areas; alternatively, they may have been eggs of E. punctifer. Miller, Watson, and Leis (1979) reported a few catches of nehu larvae in offshore areas, but always close to semiencloded areas. Anchovy larvae have occasionally been taken in large numbers 10-20 km offshore (Clarke 1983), but all specimens examined from such areas appear to be E. punctifer.

Juvenile and adult nehu are certainly abundant and most frequently encountered in enclosed areas of

Hawaii, but several lines of evidence indicate that at some time after metamorphosis, nehu may either regularly or occasionally move to offshore waters. Schools of nehu are encountered and taken by bait fishermen in shallow areas of exposed coasts that are well removed from enclosed habitats, and fishermen have reported schools of "nehu" from farther offshore. Nehu have also been found in stomachs of troll-caught scombroid fishes from offshore areas. Unfortunately, few of the offshore occurrences have been confirmed as nehu rather than E. punctifer, and even the definitely identified specimens from stomach contents could conceivably have been survivors from bait released at sea. Studies of morphometrics and meristics by Matsui (1963) and Tester and Hiatt (1952) showed little or no evidence of differences between populations from several separate areas of Hawaii and thus indicate regular interchange between enclosed areas. Recent studies in Kaneohe Bay indicate abrupt, nonseasonal changes in abundance of nehu eggs and in abundance and size composition of spawning adults. These changes could result from as yet unpredictable movements of postmetamorphic, but nonspawning nehu to offshore habitats and their subsequent return inshore to spawn.

LIFE HISTORY

Nehu spawn throughout the year. Tester (1955) concluded from egg abundance data in Kaneohe Bay that the peak spawning period occurs during the summer. Watson and Leis (1974) noted different peak periods and proposed a 56-week spawning cycle to account for the differences between their data and Tester's (1955) data. Both studies, however, sampled eggs only with surface plankton tows, and recent work has

shown that over 90% of nehu eggs occur well below the surface--usually below 5 m. Thus egg densities recorded by both studies are too low, and apparent peaks, particularly those from the Watson and Leis (1974) study, are probably meaningless and perhaps resulted from greater vertical mixing or slightly deeper excursions of the sampling nets on certain dates.

A 4-year survey of egg abundance in Kaneohe Bay using vertical net tows and a similar 2-year survey in Pearl Harbor indicate that, in most years, spawning is lowest in the late winter and spring. There is, however, a great deal of year-to-year variability in the pattern, and abrupt changes in egg abundance occur within the broad peak periods. The overall pattern agrees generally with that inferred by Leary, Murphy, and Miller (1975) from the reproductive condition of mature-sized females. To date, there are no clear correlations of spawning intensity with any environmental variable such as temperature, salinity, day length, or rainfall. Neither Tester (1955) nor current studies indicate a lunar or other regular short-term periodicity in spawning.

Yamashita (1951) concluded that nehu spawn around midnight. With more appropriate sampling, Clarke (in press) showed that spawning was concentrated in an approximately 1-hr-long period shortly after sunset. The delay after sunset is about an hour longer in summer than in winter. Tester (1951) concluded that spawning in Kaneohe Bay is concentrated in a single area over deep water in the southeast basin. More recent studies with vertical tows and higher station density show that there are two main areas where spawning is concentrated--one in the southeast basin and another in the

broad expanse of open, deep water in the middle section of the bay. Tester's (1951) conclusion that nehu eggs were most abundant near the surface seems explainable only on the basis of faulty sampling. Very limited vertical sampling by Au (1965) in Pearl Harbor showed that nehu eggs were more abundant at 2 m than at the surface. More recent data from Kaneohe Bay show that newly spawned eggs occur almost exclusively below 5 m and that even by the next morning, few have been mixed shallower.

Nehu eggs are ellipsoidal with the long axis about 2.2 times the short axis. The perivitelline space is greater at the ends than along the sides, and in freshly spawned eggs the yolk volume averages about 80% of the egg volume (Clarke, in press). Nehu eggs are almost impossible to confuse with those of any other fishes from Hawaii except those of *E. punctifer*. The only other fishes with ellipsoidal eggs are *Schindleria* spp. and scarine parrotfishes (Scaridae). Those of the former have a distinctive cap on one end, and those of the latter have a prominent oil globule, both of which are absent in nehu eggs (Watson and Leis 1974). The ellipsoidal eggs with oil globules reported by Au (1965) from just outside Pearl Harbor were almost certainly scarine eggs (which had not been described at the time of Au's study).

As with many other species of fishes, egg size changes with season. In Kaneohe Bay, eggs averaged 1.32 by 0.60 mm in winter and were about 25% greater in volume and dry weight than in summer when dimensions averaged 1.25 by 0.56 mm (Clarke, in press). There was no relation between egg weight and female size for one series of spawning adults examined. Yamashita

(1951) reported that eggs from the Ala Wai canal were smaller than those from Kaneohe Bay.

Yamashita (1951) described embryo development during incubation. He also estimated that total incubation time was about 24 hr, but varied inversely with temperature. Clarke (in press) showed that incubation time varied from about 22 hr in June and September when ambient temperatures were 26.5-27.5° C to about 35 hr in March when the temperature was 22° C.

Nehu larvae are relatively elongate. Individuals over 5-6 mm long can be readily discriminated from all other elongate larvae in Hawaiian waters based on pigment and other features described by Miller, Watson, and Leis (1979) and Yamashita (1951). Smaller larvae cannot be unequivocally distinguished from those of E. punctifer. Small larvae of the genera Schindleria, Vinciguerria, and Cyclothone resemble small nehu. These larvae normally occur in exposed coastal and offshore waters, but are occasionally advected into embayments. Careful examination of pigment pattern is necessary to discriminate these--especially for damaged individuals, but their densities in embayments are so low that any error induced from misidentifications would be minor.

At hatching, nehu larvae are slightly over 2 mm long, the notochord is bent anteriorly, and the yolk sac is still evident. Early development of larvae was described in detail by Yamashita (1951). By the time first-feeding status is reached, the larvae are about 3 mm long and straightened, the yolk sac is no longer present, the pectoral fin rays are evident, the eyes are pigmented, the gut is differentiated into fore and hind sections, and the

mouth is functional. Clarke (in press) showed that the duration of the period between hatching and first-feeding status was about 60 hr in September, the warmest month, and about 106 hr in March, the coldest month. Caudal flexion occurs at 7-8 mm length; thereafter, the larvae gradually assume adult form until metamorphosis at about 30-mm standard length (SL).

Initially, nehu larvae feed only during the daylight hours (Burdick 1969; Johnson 1982). The diet of the smallest feeding larvae is dominated by small (approximately 0.10 mm long) copepod nauplii. Nauplii are normally present at concentrations of about 100/l in the productive southeast basin of Kaneohe Bay, and both the above studies found that most first-feeding larvae had several items in the gut throughout the day. Johnson (1982) showed that gut transit time of ingested organisms is short and that daily ration of the smallest feeding nehu larvae is of the order of 40% of bodily weight.

Ecology and behavior of larval nehu between early feeding stages (3-5 mm) and metamorphosis are poorly known. The size of prey ingested increases with growth (Burdick 1969). Copepod copepodites replace nauplii as the dominant food item in larvae over 4-5 mm long, and by metamorphosis, the larvae eat prey similar in size to those eaten by adults (see below). The larvae appear to remain mostly below 5-m depth in the open waters of the bay until at least 10 mm SL (Watson 1974). Both Tester (1951) and current sampling indicate that feeding larvae tend to be more abundant by day around the periphery of deep basins of Kaneohe Bay and not in the same areas where spawning is most intense. Night feeding begins at a length of about 20 mm SL (Burdick

1969). Between 20- and 25-mm SL larvae begin on/offshore migrations similar to those of adults. Larvae 25-30 mm SL are commonly found with juveniles and adults in shallow areas by day.

Nehu metamorphose into juveniles at about 30 mm SL, but the exact size appears to vary, and some length "shrinkage" probably also occurs. Some samples contain fully transformed individuals as small as 28-29 mm SL, while in others all individuals less than 32-33 mm SL show larval or metamorphic features. Variation in size at metamorphosis appears unrelated to season or any other environmental parameter.

Late larvae, juveniles, and adults appear to perform diel on/offshore migrations. They are usually encountered by day in shallow (1-3 m deep) areas close to shore and typically near a stream mouth or other source of fresh water. The bottom is usually mixed sediment/coral rubble, and the water is usually turbid. Adult nehu are, however, occasionally encountered by day over reef areas in clear water. In such situations, they are usually more tightly schooled than when in turbid areas. What appears to be the same group of nehu (judged by size composition) may be found in the same inshore area for several days or even weeks and then disappear. Nehu may also be found in a given area in the morning and be gone by afternoon, or vice versa.

At night, nehu disperse into deeper water. There is evidence (see below) that spawning individuals may move farther away from the reef edges than nonspawners. There is also some evidence that adults may occasionally remain in deep water by day rather than moving inshore. On several occasions, inshore daytime sampling in Kaneohe

Bay has produced few or no mature fish while nighttime samples or plankton tows for eggs have indicated substantial numbers of adults present.

From the late larval stage onward, nehu feed almost exclusively at night. Night-caught nehu almost always have freshly ingested food items in their stomachs. Those from early morning samples generally have full stomachs with most of the material well-digested. Stomach fullness appears to decrease during the day. Freshly ingested benthic crustaceans are found very rarely in day-caught nehu. By late afternoon, stomachs are typically either empty or contain only a trace of well-digested food. Daily ration has not been estimated, but is probably of the order of 5-10 percent of bodily weight. Dry weight of prey from stomachs of nehu that were captured just after dark and presumably had been feeding for only about 1 hr is frequently equal to 1-2% of bodily dry weight.

Hiatt (1951) examined the diet of nehu from several localities based on samples of nehu attracted to a night light or taken in daytime beach seines. The most frequent prey items from all areas were relatively large planktonic crustaceans. His nightlight samples were probably biased by the type of food attracted to the lights, and the daytime samples probably biased toward less digestible, more recognizable forms. Both types of bias would tend to overestimate the importance of large crustaceans. Qualitative observations of stomach contents from nehu taken by "blind," nighttime purse seine sets in Kaneohe Bay indicate that relatively large crustaceans are in fact the dominant prey items, but that chaetognaths and larvacean tunicates are also frequently taken and are occasionally major fractions

of the diet. In the southeastern basin of the bay, where the diversity of macrozooplankton is low (Peterson 1975), the dominant holoplankters in the diet are the ghost shrimp Lucifer chacei and the large copepod Labidocera sp. Meroplankton, principally decapod zoeae and magalopae and large barnacle nauplii, may dominate the diet during periods when they are very abundant in the plankton. In the more seaward sections of the bay, both the diet and the macrozooplankton are more diverse and include amphipods, ostracods, and several types of larger copepods. Postmetamorphic nehu almost never consume the small (0.5-0.7 mm long) microcopepods that dominate the bay zooplankton. The smallest prey items regularly found are gastropod veligers. These are about 0.3-0.4 mm in diameter when preserved but are probably at least twice that size when alive and with their velum extended.

This information on diet indicates that nehu are particulate or "biting" feeders rather than "filterers" (O'Connell 1972) and probably attack visually detected food items individually. Their diet would be expected to vary temporally and spatially depending upon the sizes, types, and visibility of macrozooplankton present or dominant in a given situation. This feeding mode would be consistent with the observations that small plankton are rarely eaten and that, while chaetognaths and Oikopleura are at least an order of magnitude more abundant than crustaceans such as Lucifer or Labidocera in Kaneohe Bay, these gelatinous, nearly transparent forms are typically taken with only equal or less frequency than the more opaque crustaceans. The feeding mode inferred from diet composition agrees with limited observations of feeding nehu in both

the laboratory and the field. They usually strike at items from an "S" shaped position and have never been observed to "stroke and glide" with the gill rakers extended as is typical of filter-feeding clupeoid fishes.

REPRODUCTION

Female nehu reach sexual maturity shortly after metamorphosis. The reported minimum size at maturity is 35 mm SL (Leary, Murphy, and Miller 1975; Clarke 1987), but occasionally even smaller females have been found with a few vitellogenic oocytes. Maturity is, however, usually delayed. Clarke (1987) found that, while nearly all females over 40 mm SL were mature, in many samples all those under 40 mm SL were immature. In general, the occurrence of mature females that are less than 40 mm SL is highest in samples from schools dominated by small fish (30-45 mm SL) and lowest in schools dominated by fish over 45 mm SL. No quantitative studies of males have been done.

Batch fecundity of nehu ranges from about 100 eggs/spawning for a 35-mm fish to over 1,600 for a 58-mm fish (Clarke 1987). For similar sized females, values from the summer averaged about twice those from winter. Relative fecundities for summer fish ranged from 433 to 4,099 eggs/g female dry weight and for winter fish, from 496 to 2,763. For both winter and summer fish, relative fecundity increased with size; the exponents of the power functions relating fecundity to weight were 1.80 and 1.83, respectively, both of which are significantly different from unity. Based on regression equations, the predicted relative fecundities in terms of wet weight for the smallest and largest fish are, respectively, 284

and 1,043 eggs/g wet weight for summer and 195 and 542 for winter.

Although egg size is greater in winter than in summer, the larger eggs in winter do not compensate for the lower numbers then, and reproductive effort per batch is higher during the summer. For females with maximum sized oocytes, the gonad to somatic weight ratio for summer averaged 6.3% versus 4.8% in winter.

Nehu oocytes are round and translucent up to about 0.25 mm in diameter and become elongate between 0.25 and 0.30 mm. Vitellogenesis is visibly evident by 0.30 mm (long axis), and the oocytes are opaque by about 0.40 mm. Separate batches of maturing oocytes are evident soon afterwards. Based on presence or absence of postovulatory follicles or hydrated ova and diel changes in oocyte size, Clarke (1987) showed that nehu normally spawn every other day. The largest oocytes present immediately after spawning average 0.56 mm long and grow to about 0.66 mm by the next night. These reach 0.75 mm by the next afternoon and begin the process of hydration, which is completed shortly before spawning time. It is not known how long individuals spawn at this frequency, but based upon episodic changes in nehu egg abundance and in abundance and size composition of adults, the duration of spawning "bouts" could be as long as several weeks. Mature-sized females with inactive gonads are very infrequent in samples from semienclosed areas. This may mean that few females survive after a period of spawning, but could also result from females' simply leaving semienclosed areas when they are not spawning.

Both Matsui (1963) and current data indicate that the overall sex ratio of nehu is probably 1:1, but there is variation between samples

from different schools and locations. Spawning and nonspawning females segregate at spawning time (Clarke 1987), but the behavior and spawning frequency of males is not known. Vagaries of remixing between spawners and nonspawners after spawning could well explain the variability in sex ratio found between different schools.

AGE AND GROWTH

Struhsaker and Uchiyama (1976) demonstrated that growth increments on nehu otoliths are laid down daily and provided age-size data for nehu from several samples. Their composite data indicate at least two growth stanzas. Up to about 15-20 mm SL and an age of 15-20 days, the larvae appear to grow either exponentially or, at least, at a greater rate than in the later phase. After 20 mm SL, increase in size with age is slower and essentially linear. The change in growth pattern is correlated with both a change in body shape and changes in behavior and feeding of the larvae. Between 15 and 20 mm SL, the larvae become deeper bodied and begin to resemble adults in morphology. Burdick (1969) noted that larvae began to feed at night at about 20 mm, and there is current evidence that on/offshore diel migration, i.e., more adultlike behavior, begins close to this size.

Age data indicate that nehu are 60-70 days old at metamorphosis and 70-80 days old at 35 mm SL, the minimum size at maturity for females. The largest fish examined by Struhsaker and Uchiyama (1976) was 63 mm SL and 189 days old. Fish over 60 mm are very rarely encountered; the maximum size recorded in over 200 samples from Kaneohe Bay is 65 mm SL. Nakamura (1970) reported a maximum size of 75 mm, presumably

measured as total length. Apparently few nehu reach the age of 6 months. Struhsaker and Uchiyama's (1976) data indicate possible differences in growth rate between seasons and between locations, but more detailed investigations are necessary to confirm these.

Several length-weight and wet-dry weight relationships have been reported for nehu. Struhsaker, Baldwin, and Murphy (1975) gave power functions for whole (including gonads) bodily wet (WW) and dry weight (DW) in gram versus standard length in millimeters for fresh specimens from day and night samples. (The night samples tended to be made up of larger fish.) Clarke (1987) gave power functions for somatic (without gonads) dry weight (SW) versus standard length in millimeters for formalin-preserved females of similar size ranges from winter and summer samples. The preexponential factors (a) and exponents (b) for these relationships are:

Night, WW vs. SL: $a = 6.53 \times 10^{-6}$; $b = 3.109$
 Day, WW vs. SL: $a = 2.72 \times 10^{-6}$; $b = 3.366$
 Night, DW vs. SL: $a = 2.25 \times 10^{-7}$; $b = 3.606$
 Day, DW vs. SL: $a = 2.69 \times 10^{-7}$; $b = 3.584$
 Winter, SW vs. SL: $a = 3.696 \times 10^{-7}$; $b = 3.47$
 Summer, SW vs. SL: $a = 8.868 \times 10^{-7}$; $b = 3.25$

Struhsaker, Baldwin, and Murnhy (1975) reported that the dry/wet weight ratio of unpreserved nehu averaged 25%. Maginniss (1970) reported a ratio of about 22% for nehu at osmotic equilibrium with salinities between 30‰ and 100‰ of ambient seawater. Clarke (1987) reported that the dry/wet weight ratio of formalin-preserved females

without gonads was 27%; the ratio for ripe ovaries from these females was about 40%.

COMPETITORS

Two other species of small, zooplanktivorous fishes routinely co-occur with nehu in semienclosed habitats in Hawaii. The atherinid Atherinomorus (=Pranesus) insularum or iao can be found mixed with or adjacent to schools of nehu in shallow water during the day, but more typically this species occurs over reef flats in clearer water than that preferred by nehu. Iao spawn demersally over reef flats (Chase 1969) rather than in deep water. The diet of iao has not been investigated, but observations and nighttime purse seine catches indicate that iao rarely move very far from the reef edges at night and tend not to co-occur with nehu during feeding periods.

The recently introduced gold-spot herring Herklotsichthys quadrimaculatus (Clupeidae) is not restricted to semienclosed areas, but appears sporadically in large numbers, particularly during the summer and fall (Williams and Clarke 1983). Juveniles similar in size to adult nehu are encountered more frequently than adults. Co-occurrence with nehu during the day is not infrequent, but like the iao, the herring generally seem to prefer areas of clearer water than do nehu. Overlap in diet between herring and nehu is substantial; both seem to feed primarily on the same large zooplankton. Nighttime purse seine samples, however, indicate that juvenile herring tend to stay closer to reef areas and are only infrequently taken in large numbers in sets that also collect adult nehu. The overlap in nighttime distributions is, however, greater than that

for nehu and iao. Adult herring, when present in semiencloded areas, appear to be more likely to co-occur with nehu at night, but their impact on nehu is more likely that of a predator rather than a competitor (see below).

Overlap between nehu and its congener Encrasicholina punctifer appears minimal. The latter species is mostly oceanic (Ozawa and Tsukahara 1973). It has never been found among the thousands of individuals from hundreds of samples of larval through adult anchovies collected in Kaneohe Bay, but does occasionally occur nearshore in more exposed areas, sufficiently frequently that fishermen recognize it as the "gill" or "blue" nehu. Matsui's (1963) studies of anchovies from exposed areas did not clearly indicate whether or not nehu and E. punctifer frequently occur together. In exposed coastal situations, the behavior and diet of the two species are likely to be very similar, but co-occurrence and possible interactions between the two would seem to be too sporadic to have likely competitive effects on nehu populations. The same is also probably the case for other small planktivores that occur on exposed coasts (the sprat or piha Spratelloides delicatus (Clupeidae) and the juveniles of the pelagic carangids Selar crumenophthalmus or akule and Decapterus spp. or opelu).

PREDATORS

During the egg and early larval stages, nehu are subject to predation by both carnivorous macrozooplankton and small planktivorous fishes. The most consistently present and abundant large zooplankton in semiencloded areas in Hawaii are the chaetognath Sagitta enflata and the ghost shrimp Lucifer

chacei (Sergestidae). Decapod larvae, ctenophores, hydromedusae, and other carnivorous zooplankton can occasionally bloom in such areas and could contribute to mortality of nehu eggs and larvae.

Juvenile and adult nehu are normally the most abundant planktivorous fish in nehu spawning areas and, as reported for the northern anchovy Engraulis mordax (Hunter and Kimbrell 1980), are a potentially important source of mortality to their own eggs and larvae. Nehu eggs have been occasionally found in stomachs of adults taken near spawning time, but in all cases were nearly fully developed eggs from the previous day's spawning. This indicates that adults may not feed while spawning; however, the extent to which adults consume eggs later in the night after spawning has ceased is not known. Another likely fish predator on eggs or early larvae is the gold-spot herring; nehu larvae have been found in stomachs of both juvenile and adult herring.

Juvenile and adult nehu are subject to different types of predators during day and night. In shallow daytime habitats, the most frequent predatory fishes known to eat nehu are lizard fish Saurida spp., the ladyfish or 10-pounder Elops hawaiiensis, and the barracuda Sphyraena barracuda. These species all co-occur with nehu in the turbid areas usually frequented by the latter and are regularly taken with nehu in baiting operations. Small jacks--Caranx sexfasciatus; C. melampygus, and C. ignobilis--are also found in turbid areas. The latter two species are, however, much more likely to be seen attacking nehu when the latter are schooled in clearer water over reef tops (Major 1978). Other daytime predators include the noddly tern

Anous stolidus pileatus and portunid crabs.

Juveniles of the carangid Scomberoides laysan or lae are frequently found mixed with schools of nehu. In Kaneohe Bay, the greatest numbers of small lae occur during July, August, and September (Struhsaker, Baldwin, and Murphy 1975). Lae between 20 and 50 mm long feed predominately on scales, and attacks on nehu appear to go on continuously throughout the day. In experimental tanks or bait wells, attacks by lae can increase mortality of nehu, but their effect in natural, unconfined waters is unknown.

Nehu co-occur with an almost totally different set of potential predators at night in open water. In addition to adult herring, which are known to eat large nehu larvae and are probably also capable of eating juveniles, adults of the round herring or makiawa Etrumeus teres are seasonally abundant in semienclosed areas and also prey upon large larvae and small juveniles. Elops hawaiiensis, particularly the larger (30-60 cm) individuals, appear to move into deep water at night like nehu and are regularly taken there by purse seine (Clarke 1983). Based on the regular occurrence of nehu in stomachs of Elops and its abundance in semi-enclosed areas, this species is probably the single most important predator on nehu. Several pelagic or quasi-pelagic carangids also co-occur with nehu at night and are either known to or likely to prey on nehu. These include adult lae, omaka Atule mate, akule Selar crumenophthalmus, and opelu Decapturus spp. Additional potential predators in the open waters are needlefish (Belonidae) and half-beaks (Hemirhamphidae). Large schools of the latter are occasionally present in Kaneohe Bay, but

nothing is known of their feeding habits.

As mentioned previously, nehu have been found in stomachs of scombrids and other pelagic predators from exposed coastal waters, but whether this represents predation on naturally occurring nehu or released bait is not known.

DISEASES AND PARASITES

Struhsaker, Baldwin, and Murphy (1975) found that nehu were frequently infected with a protozoan resembling Cryptocaryon spp. during the warmer months (March through November). Infection, which was evidenced by white cysts on the gills, was light on freshly caught fish, but became severe in captive fish unless they were held in reduced salinities. No other investigations of diseases in nehu are known.

Hiatt and Tester (1949) gave a cursory report on nehu parasites, the most frequent of which were nematodes. Clarke (1987) found nematodes to be common in females examined for fecundity studies. Presence of these parasites had no significant effect on fecundity. Ectoparasitic isopods, identified as Family Cymothoidae by Struhsaker, Baldwin, and Murphy (1975), are found on nehu, but rarely at high frequency.

ROLE IN THE ECOSYSTEM

Nehu are the dominant small planktivorous fish in semienclosed areas (with the possible exception of short periods when large numbers of gold-spot herring are present). They almost certainly play a major role in water column processes. Adequate data for definitive

calculation of their role are not available, but very rough estimates of nehu standing crop, consumption rate, and annual production can be compared with estimates of phytoplankton and zooplankton production in the open waters of Kaneohe Bay.

Available, but incompletely analyzed, data on egg abundance indicate that the total spawning biomass of nehu in Kaneohe Bay is of the order of 1-10 tons wet weight or 0.1-1.0 tons carbon (C) over much of the year. This estimate does not include late larvae or juveniles. Based on areal data from Bathen (1968) and Smith et al. (1981), the deep-water areas where nehu forage amount to roughly 10 km^2 . The standing crop of nehu would then be $0.01\text{-}0.1 \text{ g C/m}^2$. Using an estimated primary production of $100 \text{ g C/m}^2/\text{yr}$ and 10% trophic efficiencies, the production of large carnivorous zooplankton, the main items in the diet of nehu, would be about $1 \text{ g C/m}^2/\text{yr}$. If nehu consume about 10% of their bodily weight/day, annual consumption by nehu would be $0.365\text{-}3.65 \text{ g C/m}^2/\text{yr}$ --somewhere between about one-third and three times the estimated production of prey. Total annual catch of nehu by the bait fishery in Kaneohe Bay is of the order of 10,000 "buckets"/year. Assuming a bucket contains about 5-kg wet weight (see below) or 500 g C, this amounts to about $0.5 \times 10^7 \text{ g C/yr}$ or about $0.5 \text{ g C/m}^2/\text{yr}$ of production by nehu to the fishery. This estimate does not include production by nehu consumed by natural predators.

These estimates are admittedly speculative with respect to the values selected for trophic efficiency, consumption rate, etc., but indicate that nehu probably consume either a large fraction of or more than the estimated production of larger zooplankton in the bay. The

production by nehu to the fishery alone appears commensurate with production by prey, which could result only if a good deal of the growth of nehu results from consumption of herbivorous rather than carnivorous zooplankton (a possibility for the larval stages) or if nehu spend a significant part of their life cycle feeding outside of the bay. The ratio of annual fishery production to the estimated standing stock of spawning adults is between 5 and 50. Even if the standing stock estimate is doubled to account for juveniles, only the lower ratio of 2.5 would be within the probable range of turnover rates. This also indicates that a large fraction of the standing stock is not present in the bay at any given time.

FISHERY

Nehu are the principal and preferred baitfish for the Hawaiian skipjack tuna, Katsuwonus pelamis, fishery. Older analyses of catch statistics (e.g., Yamashita 1958) from the bait fishery indicate that nehu constituted over 90% of the bait taken. Until the mid-1970's, almost all of the remaining bait taken were iao. Since its introduction in about 1975, the gold-spot herring has probably made substantial contributions to the bait catch. Recent catch data have not been analyzed, but the contribution of herring to the total bait catch is probably at least 10%. The fraction of total "nehu" catch made up by Encrasicholina punctifer is probably minor except possibly in situations like the Maui fishery where a substantial part of the yield is taken in exposed coastal waters rather than in protected areas (Matsui 1963).

Fisherman prefer nehu over all other available and tested bait

species because nehu seem to better stimulate biting by skipjack and remain close to the fishing vessel when released. Other species, including tilapia, threadfin shad, and top minnows, have been tested and either found lacking in proper bait characteristics (Brock and Takata 1955) or have not been actively sought by the fishermen. The Marquesan sardine Sardinella marquesensis was introduced as a potentially adequate supplement to nehu (Murphy 1960), but has never become abundant enough to contribute to the bait catch. The gold-spot herring, apparently accidentally introduced around 1975, has become abundant throughout Hawaii. Although its behavior as bait is said to be inferior to that of nehu, it appears acceptable to fishermen and is certainly contributing to availability of bait--especially in places and times where nehu are often available in low or unpredictable numbers. Perhaps the simplest way to illustrate fishermen's preference differences is that they will take iao only when nehu cannot be found, but will often take herring if they find them before encountering nehu. (In at least one case, however, a skipjack vessel was observed dumping a full load of herring when nehu were encountered later during the day.)

Hawaiian skipjack fishing vessels are, with one exception, wooden-hulled vessels built in the late 1940's. Each has six bait wells of approximately 2,000- to 5,000-l capacity each. Uchida (1977) has provided the most recent review of the fishery. Bait are collected by two methods. During the day, shallow inshore waters are searched from a skiff carrying a large seine. Once located, nehu are surrounded with the seine, which is then drawn up into a pocket and brought to the fishing vessel moored in deeper

water. The catch is then dipped from the net with 25-l (6 gal) buckets and transferred to the bait wells. For night baiting, the vessel is anchored in deep water--usually close to reef areas--and a lift net is suspended below a night-light. If and when sufficient numbers of nehu are attracted to the light, the latter is dimmed, and the net is lifted from below. After the net has been drawn up and the nehu concentrated, they are transferred to the bait wells in buckets. During day baiting anywhere from one to nine sets may be made per day, while usually only one "lift" per night is made during night baiting (Uchida and Sumida 1971).

The skipjack fishery is severely limited by bait availability and bait well mortality. About one-third of the fishermen's time is spent in baiting operations, and mortality in the bait well can often reach 25% or more per day (Brock and Uchida 1968). This limits the duration of fishing time between baiting operations. Some solutions to bait well mortality were suggested by Brock and Takata (1955), and the problem was more thoroughly investigated by Struhsaker, Baldwin, and Murphy (1975). The main recommendations from the latter study were to avoid damage and loss of deciduous scales during capture and transfer, to lower salinity for as long as possible after capture to minimize osmotic stress to damaged fish, and to maintain oxygen concentration at or near saturation. Although these and other recommendations have been publicized (Baldwin 1973), there has been essentially no implementation of them by fisherman.

Struhsaker, Baldwin, and Murphy (1975) also found that small nehu suffer higher postcapture mortality than large ones. In actual baiting operations, all the large larvae and

a large fraction of the small juveniles taken in the seines do not even survive to reach the vessel. Both Struhsaker, Baldwin, and Murphy (1975) and some fishermen report that night-caught nehu tend to be larger than day-caught fish and, probably as a consequence, survive better after capture. The trauma of capture and amount of handling are also less for night-caught bait.

Baitfish catch statistics are reported to the Hawaii Division of Aquatic Resources. Catch is reported in "buckets," a term derived from the (fairly) standard 25-l buckets used by the fishermen. The amount of bait per bucket, however, can vary greatly and has been reported as anywhere from 5,000 to 20,000 fish and from 3 to 10 kg wet weight per bucket (Hida and Wetherall 1977). The means from the latter study, based on 13 samples from six different net sets, were about 10,000 fish and 6.4 kg/bucket, but there was a great deal of variability between vessels and even between buckets taken from the same set. The number of fish per bucket is probably inversely related to the average size of the fish captured. More importantly, the numbers of buckets actually reported to the state are probably estimates of how many are in each well at the end of baiting rather than counts of the actual number of buckets dipped. The fishermen's ability to estimate how near capacity their wells are filled is probably more reliable than any study of numbers or weight per buckets dipped. Their estimates probably also take into account the size of fish captured and are thus probably more consistent in terms of weight than in number. For example, a bucket of 5,000 fish from a school of large (45-55 mm) nehu would weigh about the same as a bucket of 10,000 fish from a school of smaller (35-45 mm) fish. Both weights would

be about 5 kg--close to the mean reported by Hida and Wetherall (1977).

Catch data, along with location, composition of the catch (as percentage of different species), number of buckets used, and number of buckets of dead fish, are reported for each day or night of baiting operations. The only possible measure of effort is thus a "boat-day." This does not account for actual time spent searching for day bait or waiting for night bait. Time spent day baiting can vary from less than an hour when nehu are plentiful to all day when none can be found. Wetherall (1977) noted that catch per boat day is influenced by bait well capacity, which varies between boats. Fishermen cannot take more than their capacity per day and will also extend search time to avoid taking less than capacity. Consequently, catch per unit effort in buckets/boat-day would not be expected to be very sensitive to actual abundance or availability of nehu.

Bachman (1963) considered catch and effort data from the three major baiting areas for the period 1948-1960, and Uchida (1977) summarized data from the period 1960-1972. From these sources and raw catch and effort data from the Hawaii Division of Aquatic Resources for more recent years, total nehu catch appears to have varied between 18,000 and 45,000 buckets/year. For most years, the annual catch was 25,000-35,000 buckets. (Catch data from after 1980 have not yet been analyzed in detail but indicate that total catch has been declining substantially.) Prior to the mid-1960's, catches from areas other than Pearl Harbor and Kaneohe Bay on Oahu were substantial. Since then, the number of vessels baiting in these areas, particularly Maalaea

Bay on Maui, have declined, and the two major estuarine areas on Oahu have contributed over 90% of the total statewide catch. Substantial catches are reported for all months of the year, but catches from the summer (May-September), when skipjack are most plentiful, tend to be almost twice those for other months. Except for the mid-1960's, when night baiting (mostly in Honolulu Harbor and Keehi Lagoon) contributed up to 30% of the total catch, the great majority of the catch was taken by day. In recent years effort and catch from night baiting have been negligible.

Most of the changes in catch data for nehu are due to changes in effort that are unrelated to availability of nehu or even skipjack. In particular, the decline of boats in the fishery--first on the outer islands and more recently on Oahu--is probably related to economic factors. Presently, the aging vessels that are lost at sea or become too expensive to maintain are not being replaced. This is in part related to higher operating costs (particularly insurance) and closure of the cannery in Honolulu. Even less obvious factors such as differences between vessel captains or the home port of the vessel appear to enter into choice of baiting in certain areas or preference for day or night baiting.

Analyses of catch per effort data have not indicated any clear trends in nehu abundance or availability, nor have they provided adequate assessment of the impact of the fishery. Bachman (1963) found some indications of short-term declines in adjusted catch per effort data from earlier years, but neither these trends nor other variability in catch per effort seemed clearly related to effort as would be expected if the fishery seriously

impacted the population. Bachman (1963) was able to derive a reasonable estimate of maximum sustainable yield only for the Pearl Harbor fishery; the previous yields from Pearl Harbor were all well below this estimate. Wetherall (1977) concluded that if catch per effort were a measure of relative abundance, the data from Kaneohe Bay indicated no relationship to the fishery. He suggested that catch per effort may measure only availability to the fishery rather than relative abundance and cautioned that better catch and effort data and understanding of nehu biology were needed to properly consider the impact of the fishery.

Recent studies suggest that nehu may move in and out of semienclosed areas. If true, this requires that analyses of the fishery will have to be approached on a statewide basis and that catch per effort may be related only to availability of nehu to present baiting methods and not to abundance. Preliminary analyses of data from recent studies in both Pearl Harbor and Kaneohe Bay indicate that a 1- or 2-month catch by the fishery is about equal to the estimated standing stock in the study areas. This means that either nehu productivity and turnover is exceedingly high or that a sizable unsampled and unexploited fraction of the population exists elsewhere.

ENVIRONMENTAL REQUIREMENTS

Most data on physiological tolerances of nehu are from Struhsaker, Baldwin, and Murphy's (1975) investigation of mortality in simulated bait-well situations. The fish had recently been stressed by capture and transport and were held at relatively high densities. The stresses and responses of nehu under these conditions are probably

unlikely to occur in nature, and the actual tolerance ranges are either likely to be broader or unlikely to be encountered in the wild.

The range of temperature encountered by nehu in both natural and bait-well situations is 18-30° C and appears to be within their upper and lower lethal temperature limits. At the higher temperatures, however, stress from other factors may be increased.

Maginniss (1970) determined salinity tolerances of nehu after a few days of acclimation to captivity. Nehu transferred directly from 100% seawater to 100% fresh water died within a few hours. Those transferred to 20% seawater survived longer, but mortality was significantly higher than of controls held at 100% seawater. Bodily water content increased initially and then declined but did not return to control levels. At 30%, 40%, and 60% seawater, survival did not differ from that of the controls. Bodily water content of nehu at 30% seawater returned to control level after an initial increase. At 40% and 60% seawater, water content never departed from control levels. In the wild, unstressed and unconfined nehu are unlikely to ever be exposed to lethal or even deleterious salinities for an extended period.

Struhsaker, Baldwin, and Murphy (1975) found that nehu are able to regulate oxygen consumption down to 2.0-3.0 ml O_2/ℓ . Below these levels, consumption decreased with dissolved oxygen concentration until a lethal concentration was reached in the 1.0-2.0 ml/ ℓ range. Their average lethal concentration, 1.44 ml/ ℓ , was lower than that reported by Pritchard (1955) for individual fish. As with the above environmental parameters, it seems

unlikely that unconfined nehu ever encounter deleterious oxygen levels in nature. Struhsaker, Baldwin, and Murphy (1975) also found that decreased pH affected nehu mortality. Stress was observed at about pH 7.5, and mortality rates increased greatly as pH approached 7.0-7.1. Again, it is unlikely that nehu would ever be exposed to such values in nature.

As mentioned previously, nehu seem to prefer relatively turbid water during the day and, except perhaps for extreme situations such as near stream mouths during heavy rainfall or in the immediate vicinity of dredging operations, are probably not affected by high concentrations of suspended material. Some fishermen, in fact, feel that nehu are actually attracted to the general vicinity of dredging or areas where vessel traffic continually resuspends sediment. Dredged channels a few meters deep across fringing reef areas also appear to provide favorable daytime habitat for nehu, and they are frequently sought in such areas by fishermen. In very shallow water, nehu are obviously disturbed and probably made more vulnerable to some predators by frequent small boat traffic, but otherwise seem little affected by nearby human activity. They are frequently found in small boat harbors and marinas.

The semiencloded areas in which nehu are frequently found are subject to eutrophication due to increased nutrient input from sewage discharge or runoff. The effects of eutrophication on Kaneohe Bay ecosystems have been the subject of a number of studies including that by Smith et al. (1981), which compared conditions before and after a major sewage discharge was diverted from the bay. Unfortunately, nehu were not included in this study. Nevertheless, there is little

evidence that eutrophication affected the population. Kaneohe Bay was a relatively productive area even before sewage discharge began and remained so after the sewage was diverted. Catch per unit effort of the bait fishery appears to have fluctuated independently of sewage discharge or divergence. Unpublished data from nighttime purse seine samples indicate no gross differences in nehu abundance between prediversion and postdiversion periods. Zooplankton or ichthyoplankton studies done before diversion were mostly inadequate for rigorous comparison with recent data on nehu egg abundance; however, counts from a few series of vertical samples taken before sewage

diversion indicate that maximum egg abundances then were similar to those observed 10 years after diversion.

Other than Welsh's (1949, as cited by Nakamura 1970) reports of nehu mortality and exclusions from parts of Hilo Bay due to industrial and sugar mill effluents, there are no data on the potential effects of other pollutants such as petroleum products, heavy metals, pesticides, etc., on nehu. Populations in Pearl Harbor and Honolulu Harbor would be most likely exposed to such pollutants due to industrial activities on the shoreline, high vessel activity, and, for Pearl Harbor, substantial runoff from agricultural areas.

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